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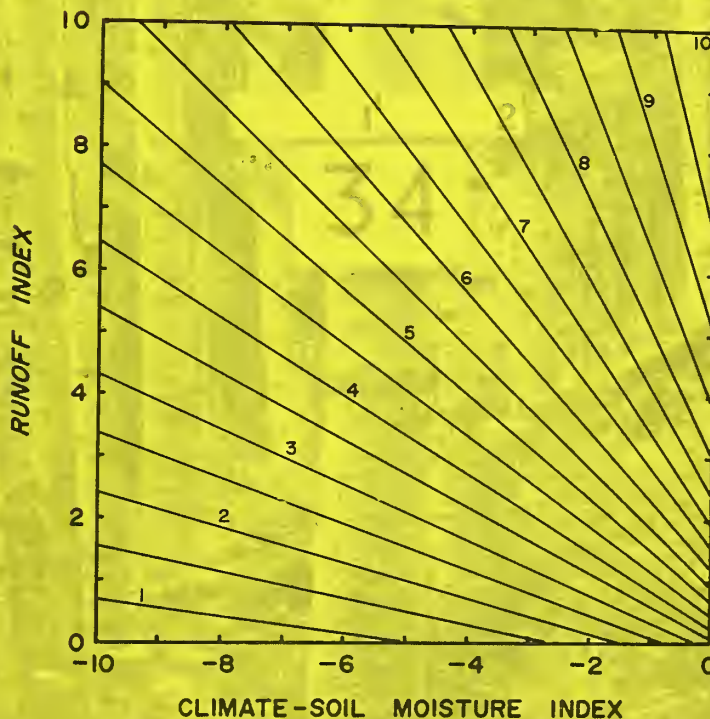
AN EXPERIMENT IN MODELING ROCKY MOUNTAIN FOREST ECOSYSTEMS

by John R. Jones

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ABSTRACT

This prototype model consists of a temperature regime ordinate, a moisture regime ordinate, and a regression equation relating them to aspen site index in the Southern Rocky Mountains. Its construction required a close look at a number of problems and considerations, and some possible methods, in ecosystem modeling. Clonal variation in aspen height growth prevented a good test of the model, however.

The temperature regime ordinate is analogous to degree-days, and integrates elevation and latitude within subregions. The moisture regime ordinate integrates estimates of monthly precipitation, monthly mean temperatures, potential direct-beam insolation, water-holding capacity of the soil, and factors influencing runoff.

Equations are provided for estimating mean monthly precipitation, based on topographic and other factors.

Key Words: Ecosystems, modeling, Southern Rocky Mountains, moisture regime, temperature regime, site index, precipitation estimates

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~~9/21/71~~ An Experiment in Modeling
Rocky Mountain Forest Ecosystems¹

by

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¹This paper is based on a dissertation presented to Colorado State University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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An Experiment in Modeling Rocky Mountain Forest Ecosystems

John R. Jones

INTRODUCTION

Soil-site equations have been made for decades and some have been quite effective. Although they are models of ecosystems, designed specifically to express environmental effects on the height growth rates of dominant trees, they are strictly empirical and do not pretend to be analogs of ecosystems. They make very little use of knowledge about how environmental factors interact to influence growth. Their central assumptions are that assorted interacting factors can be treated as statistically independent, with additive effects, and that where interactions are recognized they are reflected by their arithmetic products. Because those assumptions are mostly untrue, a narrow limit is set on the number of factors that can be included in the model. An implicit corollary assumption is that the factors used are adequate.

An alternative kind of ecosystem model is structured theoretically, with the factors integrated in the model in the way they are thought to interact in nature. Available data are used to develop the constants in the relationship. The central assumption is that we know enough about the ecosystems to make a model that works effectively.

In 1961 I was assigned to develop a soil-site equation for quaking aspen (Populus tremuloides Michx.) in the Rocky Mountain Station territory. The literature on soil-site studies (Jones 1969) emphasized the importance of confining a soil-site study to an area with an essentially homogenous macroclimate. The Rocky Mountains hardly qualified. It appeared that climate would have to be included in the model.

That was done by developing a model integrating climate, soil, and topography in a way that seemed analogous to their interactions in nature.

Bakuzis (1959) and Loucks (1962) modeled the environment as a multi-dimensional space defined by ordinates. Three of Bakuzis's ordinates—moisture regime, temperature regime, and nutrient regime—seemed appropriate for my needs. It developed that some plots among

the lowest in nutrient status had fair to very good aspen site indexes, however, so a nutrient regime was not constructed.

Rather than using vegetation composition to assign coordinates, as Bakuzis did, I used Loucks' approach. He integrated physical site factors to define his ordinates. But his purpose was to relate vegetation to habitats, and he was working in a single New Brunswick watershed. My purpose was different and my study area enormously more varied, so my methods had to be different.

Models usually are tested by comparing their output to output by the real system. The output against which I planned to test my model was aspen site index. It developed later, however, that different aspen clones growing next to each other on the same site can have considerably different site indexes.³ Therefore aspen site indexes do not provide a good test for the model.

Even untested, however, the model serves a useful purpose. Description of its construction gives a close look at many of the problems and considerations, and some possible methods, in modeling forest ecosystems.

The area that the model represents is primarily Fenneman's (1931) Southern Rocky Mountain (physiographic) Province, but also includes adjacent forested uplands of the Colorado Plateau Province and the Great Plains and Wyoming Basin Provinces (fig. 1).

TEMPERATURE REGIME ORDINATE

Effects of Temperature on Height Growth

In modeling the temperature regime, the temperature effects considered were those essentially not part of the hydrologic cycle. The effects of temperature on moisture supply were considered in modeling the moisture regime.

Temperature affects the intensity level of most physiological activities. Different activities, for example photosynthesis and respiration, may have very different temperature response curves (Tranquillini 1955).

³The subject is reviewed by Jones (1967).

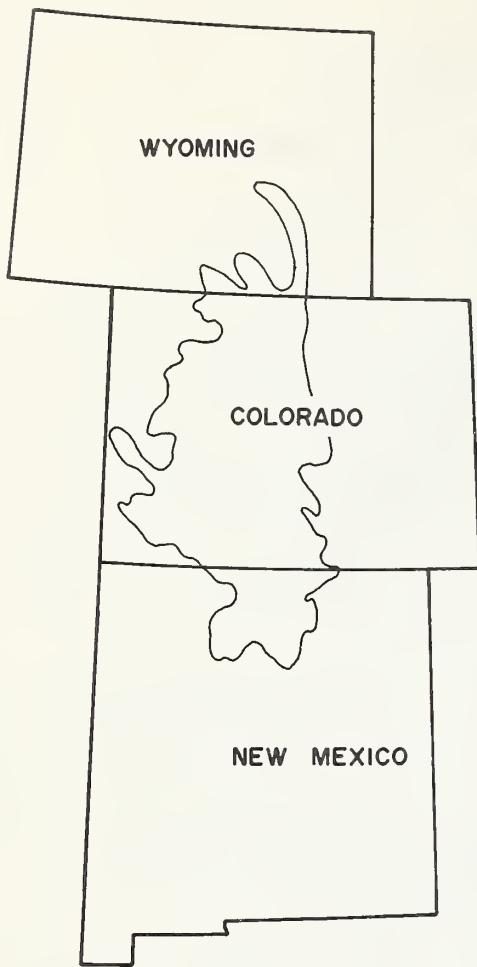


Figure 1.--The Southern Rocky Mountain Region as defined for this study (enclosed by irregular line).

Height growth is a complex activity; its temperature response surface integrates the varying responses of a number of basic physiological activities. Apparently, height growth rate as a function of temperature has not been worked out for any tree species beyond the early seedling stage.

Lovcic (1962) found evidence that the very low temperatures of the 1939-40 winter in northern Russia caused reduced diameter growth for the subsequent 3 to 5 years. In the present study, it was assumed that winter minimums seldom if ever affect the height growth of native trees in the Southern Rocky Mountains.

Gates (1968) pointed out the importance of transient temperature fluctuations to organisms. Too little is known to consider the effects of transient fluctuations here, however. Instead it will be assumed that the effects of periodic and nonperiodic temperature fluctuations do not differ from place to place where general temperatures are similar, so far as the height growth of indigenous trees is concerned.

Air temperature can usefully be regarded as a base from which plant temperatures vary. For our purposes, heat released by the chemical activities of the plant is insignificant (Meyer and Anderson 1952, p. 396). During the daytime, the amount of radiation absorbed by the plant surface and the rate at which that energy is disposed of largely determines how much tissue temperatures will differ from air temperature.

It is assumed here that in forest stands the important temperature effect of summer radiation is on leaves. Stems normally are more or less shaded in summer. Furthermore, the outer bark, with its low thermal conductivity, intercepts the radiation reaching the stem and reduces the energy reaching the phloem and the vascular cambium. Roots, of course, are shielded from insolation by the (usually shaded) soil with its low thermal conductivity, and experience a conservative temperature regime (Jankovic 1962).

Clouds have an important effect on radiation intensity, but it is not clear how variable average summer cloudiness is from place to place in the Southern Rocky Mountains. Certainly clouds are abundant in summer even over the driest part of the region—the San Luis Valley with its 6 to 7 inches of annual precipitation.

At any rate, the effectiveness of insolation in raising leaf temperature probably is most often determined by the rate of heat dispersion. Evaporation, back radiation, conduction, and even convection all are negative feed-back mechanisms; the greater the energy received by the leaves the more rapidly it is disposed of. Wind tends to speed cooling by sharpening the gradients of temperature and vapor pressure near the leaf. Even with transpiration stopped experimentally, the temperature of strongly irradiated leaves was reduced to near air temperature by a small amount of wind (Reifsnyder and Lull 1965, p. 66).

There is no basis for dealing with wind in this study. The consequences of ignoring it depend on whether daytime cooling by wind varies importantly from place to place within the region. Actually, wind cooling of plants is not a linear function of wind. Gates (1968) showed that, during the growing season in the Southern Rocky Mountains, winds of 2 miles per hour are enough to bring leaf temperature close to air temperatures. Stronger winds have little additional temperature effect. It is doubtful that calms are frequent or of appreciable duration during the day at the upper crown levels of aspen forest in the region.

In constructing the temperature regime ordinate it was assumed that (1) air temperature, radiation, and wind are the keys to aspen temperature in the Southern Rocky Mountains, and (2) the temperature effects of radiation and wind on aspen site index do not vary importantly from place to place within the region. The temperature ordinate consequently will consist simply of an air temperature index.

Air Temperature Index

A heat sum is the sum of daily average temperatures above some threshold temperature. Went (1957, p. 224) stated that the relation between plant growth and heat sum is not linear but usually is expressed more adequately as a cubic function:

$$g = a + bt + ct^2 + dt^3$$

g representing growth, t temperature, and a - d constants, d always being negative. This function expresses the sigmoid response curve typical of many biological activities.

Went did not believe this function is useful for expressing field behavior, however. Among his reasons were:

1. The parameters are not constant throughout the growing period.
2. "Since heat is not a form of available energy for plants, and only modifies other processes, it is logically impermissible to talk about—or even calculate—heat sums."

But Lanner (1964), working with 4-year-old knobcone and digger pines, concluded that the use of heat sums is appropriate where growth rate is closely tied to chemical reaction rates. As a general rule the height growth of trees varies with both the warmth and the length of the growing season (Paterson 1956), presumably through their effect on biochemical reaction rates. This amply justifies the use of heat sums.

Both Armson (1962) and Lanner (1964) found the height growth of coniferous seedlings exponentially related to heat sums. Many such exponential functions approach linearity over an important part of their range, however.

In some regions, normal heat sums for heights above about 5 feet can be estimated for a study area simply by using data from the nearest weather station. In the Rocky Mountains, however, the climate of a temperature station only 10 miles from the study area may be radically different.

A regression equation for estimating heat sums from elevation and latitude could be developed from published mean temperatures, but it would involve an important bias. A

disproportionate number of weather stations in the region are located in valleys or at the foot of mountain ranges, and are subject to strong nocturnal temperature inversions. Because of the abnormal minimums, their average temperatures are somewhat lower than on mountain slopes at similar elevations.

Temperature maximums a few feet above open ground are less affected by terrain than are minimums (Jackson and Newman 1967); in the Rockies, considerably less. What might be the result of ignoring minimums—of using maximums alone instead of means to characterize the air temperature macroclimate?

In this region, aspen stands occur mainly above 8,000 feet. At those elevations nighttime temperatures in summer ordinarily drop below 50° F., and occasionally below freezing in valley bottoms. Tranquillini (1955) found that night-respiration rates of young *Pinus cembra* (4-17 years old) in the Alps were almost as low at 50° F. as at the freezing point. If respiration is regarded as the limiting growth factor at night, perhaps the different minimums in Southern Rocky Mountain forests do not differ importantly in their effects on height growth. An exception would be hard frosts, for example 25° F., which affect the structure of plastids and other protoplasm and reduce photosynthesis temporarily (Tranquillini 1964). Another exception would be frosts severe enough to damage the growing points of stems.

Therefore, to reduce the problem of bias in weather station locations, maximums were used instead of means. A threshold temperature was subtracted from the normal daily maximum for each month. The sum of positive monthly values, closely analogous to a heat sum, is called here the air temperature index.

The threshold temperature used, 45° F., was obtained by compiling a list of high-elevation weather stations and plotting their average daily maximum temperatures for July over elevation. The curve was extrapolated to 14,400 feet—approximately the height of the highest peaks in the region. Theoretically this threshold value should also provide positive air temperature indexes for alpine studies.

In general, aspen buds do not open in the Southern Rocky Mountains until the course of maximum temperatures rises above about 55° to 60° F. Therefore it could be argued that 55° or 60° would have been a better choice. However, when temperature indexes based on a threshold temperature of 58° F. were graphed over temperature indexes for the same weather stations based on 45° F., a close linear relationship was found. Therefore growth should have the same regression slope on temperature index whichever threshold is used.

Air temperature indexes can be estimated from latitude and elevation for plots in any of three subregions. The subregions are shown in figure 2 and described in the appendix. The estimating equations, with their standard errors of estimate ($S_{y \cdot x}$) and coefficients of determination (R^2) are:

Western subregion:

$$Ti = 592.5 - 3.59 L - 0.0931 EL$$

($S_{y \cdot x} = 10$; $R^2 = 0.96$)

Eastern subregion:

$$Ti = 800.3 - 9.76 L - 0.0800 EL$$

($S_{y \cdot x} = 15$; $R^2 = 0.91$)

Southern subregion:

$$Ti = 507.2 - 0.1105 EL$$

($S_{y \cdot x} = 14$; $R^2 = 0.86$)

where Ti is temperature index, E is elevation in hundreds of feet and L is latitude in degrees and tenths.



Figure 2.--
Subregions for temperature equations.
Dense stippling--eastern subregion.
Open stippling--southern subregion.
Clear--western subregion.

Ti estimates usually are close at lower forested elevations—7,000-8,000 feet—which are near the mean elevation of the stations used in developing the equations. They are usually fairly close at subalpine and upper montane elevations (the major forest zone) and for the plains.

Considering the derivation of the threshold temperature, Ti might be expected to equal zero at about 14,400 feet. Using average subregional latitudes, however, estimated Ti drops to zero at 12,600 feet in eastern Colorado, 12,700 feet in northern New Mexico, and 12,900 feet in western Colorado. It is not clear whether this is due to extrapolating the estimating equations or whether it results from extrapolating the curve of temperature over elevation to get the threshold temperature.

MOISTURE REGIME ORDINATE

Selection of Factors

Precipitation varies greatly from place to place in the region, and so does the water-holding capacity (WHC) of the soil. Soil texture and depth, two important elements of WHC, have been widely used in soil-site studies and usually prove closely related to tree growth (Jones 1969). WHC should be especially important in areas with marked periodic precipitation deficits during the vegetative season.

After moisture has fallen it may be redistributed from one site to another as runoff, mainly within the substrate. Water gained or lost by runoff often is important to the moisture supply on a site (Gysel and Arend 1953, Trimble and Weitzman 1956, Hewlett 1961a, Hewlett and Hibbert 1963, McDonald 1967). This should be especially so in mountainous regions with periodic moisture surpluses and deficits.

Evaporative stress, the other side of water balance, is a function of vapor pressure gradient and therefore of air temperature, radiation, humidity, and wind (Lowry 1969). Useful data on humidity and wind are not available in the mountains, however, even at most weather stations.

The variables combined in the moisture regime ordinate are precipitation, water-holding capacity of the soil, air temperature, insolation, and runoff.

Precipitation

Within the region, normal annual precipitation at weather stations is as low as 6.56 inches at Alamosa, Colorado, and as high as

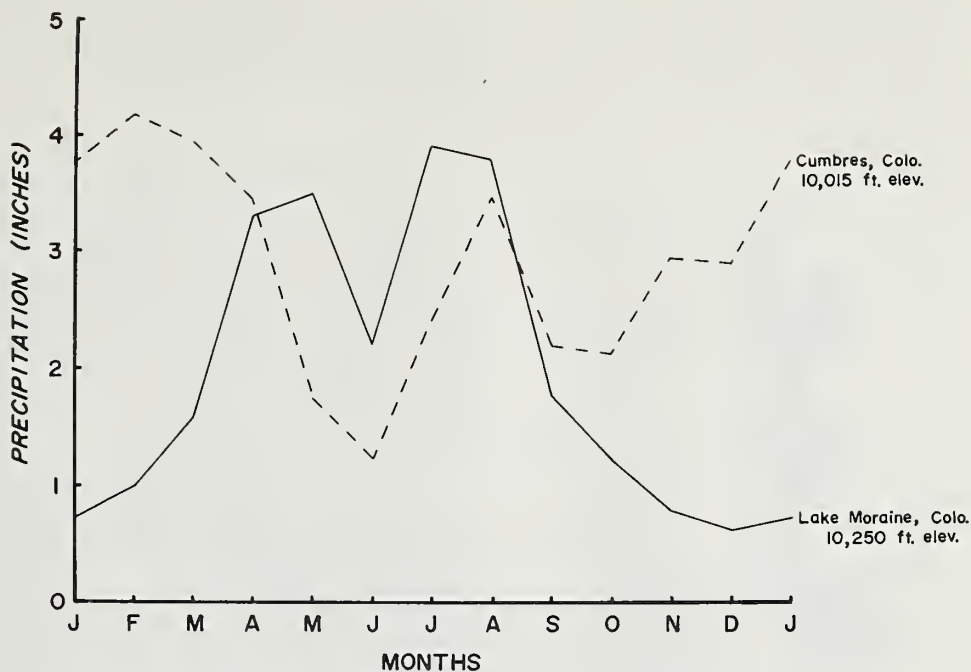


Figure 3.--Seasonal distribution of precipitation at two subalpine weather stations at similar elevations.

44.04 inches at Wolf Creek Pass 4W, Colorado. Normal precipitation on aspen forests seems to range from more than 45 inches a year in the wettest areas to less than 15 inches in the driest.

A number of factors influence normal precipitation, interacting and changing their relative importance from season to season. As a result, the pattern of seasonal distribution differs from place to place, as demonstrated by records from two stations of very similar elevation (fig. 3). The seasonal distribution of precipitation influences its effectiveness and the importance of terrain and storage. Therefore, seasonal or monthly precipitation values express the precipitation climate more usefully than do annual values. Tables by Thornthwaite and Mather (1957) offer a way that is both reasonable (Penman 1963, p. 40, 49, 60; Fraser 1966) and feasible to integrate moisture income and loss. They were used in this study to develop the moisture regime ordinate, and require monthly values of precipitation.

No monthly isohyetal maps of the region were found, so regression equations were developed for estimating monthly precipitation. The approach was provided by Spreen (1947) who constructed a graphical system analogous to multiple regression to estimate winter precipitation in western Colorado. In the present

study, 134 weather stations were used in or immediately adjacent to the region. For each, a number of topographic variables were read from maps and analyzed graphically for their relation to monthly precipitation. Precipitation values were the observed norms for 1931-60, or averages for some other period normalized to a 1931-60 base as described by Landsberg (1962, p. 91). Based on the graphical analyses, more than 20 expressions of those variables were defined, and screened by stepwise multiple regression analyses for their relations to monthly precipitation. The variables retained for the final analyses were: elevation (E), latitude (L), relief (R), barrier (B), and subregion. E expresses orographic effects and L expresses position relative to normal monthly storm tracks. R is the superiority of elevations within 3 miles of the weather station to the elevation of the station, expressing approach and canyon effects and to some extent topographic boosts to convection. B is the superiority of elevations in each of six compass sectors at distances of 10 to 100 miles tending to intercept moist air, and expresses the rain shadow effects of mountain ranges in or near the region. Subregion expresses effects of barriers or their absence at a distance from the region. The variables are described more completely in the appendix. Precipitation subregions are shown in figure 4 and described in the appendix.

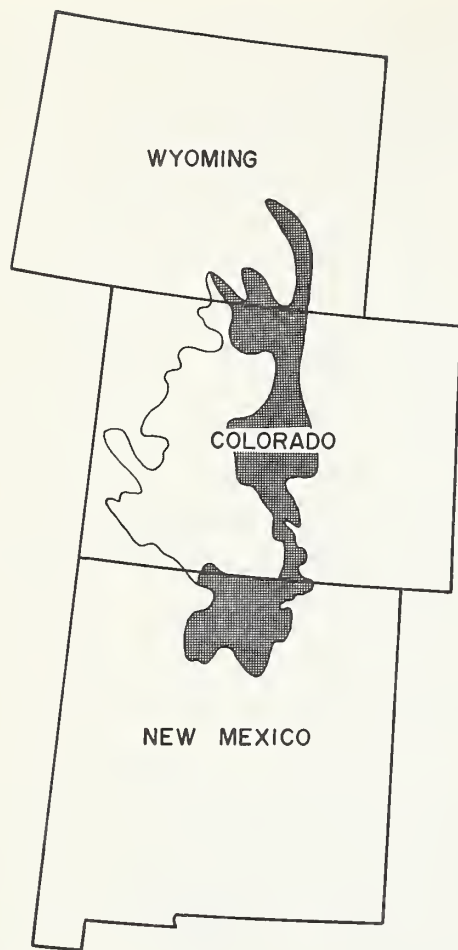


Figure 4.--
Subregions for precipitation equations.
Stippled--eastern subregion.
Clear--western subregion.

Trial graphs and calculations suggested that precipitation varied more or less linearly with elevation and relief, but exponentially ($n < 1$) with barrier. Had more stations been available above 9,000 feet the relationship with elevation probably would have been nonlinear.⁴ Theoretical monthly exponents for barrier were determined from published data (U.S. Weather Bureau 1951) on changes in amounts of precipitable water with elevation. The exponents fall into three groups, centered around 0.3 for the winter months (December, January, and February), 0.5 for summer and early autumn (June, July, August, September, and October), and 0.4 for the intervening months (March, April, May, and November). Trial regressions indicated

⁴Letter from Arthur Judson, Associate Meteorologist, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, August 15, 1969.

that these theoretical exponents are appropriate to the study data, and they were used with B in the final regressions (table 1).

Water-Holding Capacity of the Soil

WHC is largely a function of soil depth, stoniness, bulk density, and texture.

Soil depth was defined as the vertical depth in inches to bedrock, to a strongly massive layer within the mantle (Lutz 1952), or to a water table restricting root growth, but in no case deeper than 72 inches. Layers that were massive but not strongly massive were considered part of the soil.

A few vertical aspen roots will penetrate even very strongly massive soil horizons as well as fractures in bedrock, and some penetrate deeper than 72 inches. Gifford (1964) traced an aspen sinker root to 114 inches where it broke! I found very few lateral roots below 50 inches, however, even in easily penetrable material.

Sixty inches was considered as a possible maximum soil depth in defining WHC, but Brown and Thompson's (1965) data on aspen and spruce water uptake from below 4 feet suggested that 72 inches is more appropriate.

Stone in the soil was regarded as waste space in figuring WHC. For each pit the volume of stone larger than gravel was calculated from weight and specific gravity. The percentage of gravel in the soil was usually simply estimated, but sometimes the gravel was screened.

Bulk density is difficult to measure in soil that is stony or has abundant tree roots. It was not treated as a variable in this study.

The soil texture of each horizon was determined by the hydrometer method.

WHC of each horizon was estimated as follows: WHC per inch of soil was read for the appropriate textural class from a table adapted from Broadfoot and Burke (1958). That value was multiplied by horizon thickness corrected for stone. It was then corrected for massive layers.

In the soil profiles observed, lateral roots often were at least somewhat numerous in nonmassive horizons to about 40 inches and sometimes deeper. At boundaries with shallow massive layers they commonly decreased abruptly. Sites with massive layers at shallow depths typically bore stands of poor or mediocre height growth rates. It was inferred from this that moisture in massive layers is less available than moisture in more penetrable layers because of restricted root distribution. For

Table 1.--Constants, standard errors of estimates ($S_{y \cdot x}$) and coefficients¹ of determination (R^2) for monthly precipitation-estimating equations,² western and eastern subregions

Independent variables, ³ $S_{y \cdot x}$ and R^2	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
<u>Western Subregion</u>												
P-intercept	-5.91	-6.07	-8.06	2.60	-3.85	-6.45	-3.47	6.60	1.96	2.07	-6.22	-6.35
Elevation	.0161	.0227	.0269	⁴ .0017	.0095	.0057	.0230	.0182			.0160	.0099
Latitude	.2036	.1887	.2265		.1423	.1881	⁴ .0992	-.1543			.1755	.2195
Relief	.0381	.0393	.0425	.0305	.0192	.0156	.0234	.0301	.0337	.0337	.0233	.0335
B^n_n				-.3071								
B^n_{ene}				-.2526	-.2349							
B^n_{ese}						-.0808						
B^n_s	⁴ -.2805						-.1541		-.0881	-.0686		-.2273
B^n_{wsW} ⁵	-.6345	-.8488	-.5231		-.0972			-.1225	-.1249	-.1665	-.3089	-.6149
$S_{y \cdot x}$.56	.61	.69	.54	.29	.19	.34	.38	.36	.40	.39	.43
R^2	.66	.66	.65	.68	.74	.74	.80	.74	.63	.60	.66	.69
<u>Eastern Subregion</u>												
P-intercept	0.82	1.11	-2.24	-5.23	-0.61	-2.10	5.72	10.41	1.86	1.58	.18	.97
Elevation	.0135	.0150	.0110	.0098			.0170	.0155			.0105	.0101
Latitude			.0907	.1725	.0841	.1022	-.1182	-.2445				
Relief			.0283	.0458	.0307	.0201	.0197	.0216	.0082	.0143	.0103	
B^n_{wnw} ⁶	-.3769	-.3993	-.1854									-.3696
$B^n_{wnw} \times B^n_n$				-.0261							-.0234	
B^n_n			-.1420									
B^n_{ene}		-.1553		-.2236	-.3710	-.0701				-.0372		
$B^n_{ene} \times B^n_{ese}$							-.0204					
B^n_{ese}							-.0693					
$B^n_{ese} \times B^n_s$								-.0217	-.0139			
B^n_s						-.0728	-.0909					
B^n_{wsW}									-.0842	-.0837		
$S_{y \cdot x}$.31	.37	.37	.42	.38	.25	.38	.40	.23	.22	.25	.27
R^2	.70	.66	.68	.74	.71	.69	.67	.71	.57	.49	.59	.70

¹Coefficients statistically significant at 5 percent level except those indicated by footnote ⁴.

²Equations have general form: $P = a + b_1E + b_2L + b_3R + b_4B^n$. . . , where $a = P$ -intercept; $b = a$ coefficient; $E =$ elevation; and so forth. For example, for January--

Western subregion: $P = -5.91 + 0.0161E + 0.2036L + 0.0381R - 0.2805 B^n_s - 0.6345 B^n_{wsW}$

Eastern subregion: $P = 0.82 + 0.0135E - 0.3769 B^n_{wnw}$

³Includes precipitation intercept.

⁴Probability about 6 percent ($t > 1.9$ for 64 observations).

⁵Barrier value for west-southwest sector, raised to a power n .

⁶Barrier value for west-northwest sector, raised to a power n .

this reason, WHC in massive layers was discounted by two-thirds. The total WHC of a soil was taken as: WHC of nonmassive layers plus 1/3 WHC of massive layers.

Air Temperature

To use Thornthwaite and Mather's (1957) water balance tables to express the moisture relations of a site, it is necessary to know the monthly mean air temperatures of the site. Because monthly isothermal maps are not available for the region, regression was used to estimate monthly means.

Published means would provide substantially biased regressions, however, because most weather stations in the region are in nocturnal cold air sinks. The abnormal average daily minimums of those stations lower the monthly means so they are not analogous to the conditions represented by Thornthwaite and Mather's tables.

Published monthly mean temperatures average the daily maximums and minimums. Put differently, the published monthly mean equals

the average daily maximum minus half of the average daily range.

Average daily ranges were tabulated from six mountain weather stations with free nocturnal air drainage. For a given month these were fairly similar, and the average daily range of the six stations for any month was used as the "standard daily temperature range" for that month. Then for each temperature station in the region, a synthetic mean temperature was calculated for each month by subtracting half of the standard daily temperature range for the month from the average daily maximum.

Such synthetic means are not strictly analogous to the conditions represented by Thornthwaite and Mather's (1957) tables, either, but probably come closer to them than do the published means. They should better represent the conditions on mountain slopes and tablelands and in most canyon bottoms, although they are no doubt inferior for representing valley bottoms.

For each of three subregions (fig. 2), synthetic monthly mean temperatures were used to develop the multiple regressions of monthly mean temperatures on elevation and latitude (table 2).

Table 2.--Multiple regressions¹ ($T = a + b_1L + b_2E$) of monthly mean temperature (°F) on latitude (0.1°) and elevation (hundreds of feet)

Month	Western subregion					Eastern subregion					Southern subregion				
	a	b ₁	b ₂	S _{y·x}	R ²	a	b ₁	b ₂	S _{y·x}	R ²	a	b ₁	b ₂	S _{y·x}	R ²
Jan.	123.8	-2.12	-0.26	2.26	0.73	191.2	-3.59	-0.30	2.34	0.88	88.5	-1.11	-0.26	2.79	0.41
Feb.	128.1	-2.00	-.32	2.17	.81	185.7	-3.33	-.33	1.91	.92	100.8	-1.12	-.37	2.28	.68
Mar.	149.6	-2.19	-.43	1.88	.91	183.6	-3.08	-.38	1.84	.93	71.6		-.45	1.97	.79
Apr.	147.9	-1.77	-.47	1.50	.95	154.5	-2.05	-.42	1.89	.93	113.2	-.85	-.47	1.40	.90
May	136.6	-1.25	-.47	1.55	.94	153.6	-1.83	-.41	2.38	.88	128.3	-1.06	-.46	1.62	.86
June	145.8	-1.28	-.47	1.46	.95	151.3	-1.61	-.38	2.04	.89	128.6	-.88	-.43	1.64	.84
July	129.6	-.65	-.49	1.27	.97	120.7	-.65	-.38	1.85	.90	102.6		-.46	1.97	.80
Aug.	124.0	-.59	-.47	1.21	.97	114.7	-.52	-.39	1.99	.89	99.2		-.43	1.68	.83
Sept.	122.4	-.79	-.42	1.51	.94	138.7	-1.36	-.35	1.94	.88	92.2		-.41	1.56	.83
Oct.	117.7	-1.03	-.38	1.63	.91	157.3	-2.11	-.33	1.98	.89	80.4		-.38	1.54	.82
Nov.	128.7	-1.84	-.31	1.45	.90	178.5	-2.99	-.33	2.04	.90	86.9	² -.70	-.30	2.10	.61
Dec.	111.4	-1.72	-.25	2.08	.74	183.7	-3.31	-.31	2.34	.87	100.9	-1.38	-.25	2.80	.40

¹Standard error of the estimate (S_{y·x}) in °F; coefficient of determination (R²)--the decimal portion of the total variance in monthly mean temperature, which is accounted for by the significant independent variables.

²0.05 < P < 0.10. All other coefficients given have probabilities of 0.05 or less.

Direct Beam Insolation

Direct beam insolation seems clearly to be the principal radiation variant, and one that could rather readily be integrated into a moisture regime ordinate.

The direct beam insolation received by a plane above and parallel to the forest canopy varies with the angle of incidence (a function of latitude, date, slope, and aspect), attenuation of the solar beam, and topographic obstructions (Reifsnyder and Lull 1965, p. 14). Attenuation varies with the optical airmass, the amount and composition of turbidity, and cloudiness (Reifsnyder and Lull 1965, p. 21-23), which differ from time to time at any place as well as from place to place at any time. It also varies statistically from place to place with cloudiness, but that statistical variation probably is not great within the region for places of similar monthly precipitation.

On some sites topographic shading reduces insolation substantially. Topographic sunrise and sunset could not be determined with instruments because the horizon could not be seen in the forest. Nor, in some areas, could they be determined from topographic maps of the quality and scale available. Therefore, topographic shading was reluctantly ignored.

In this study a single variable, "potential direct beam insolation," was used to represent the radiation environment. Potential direct beam insolation is the daily direct beam solar radiation in langley (ly) that would be received by a plane above the crown canopy and parallel with plot surface if the atmosphere were perfectly transparent. Daily values in ly for 16 compass points and a wide range of slopes, aspects, and latitudes can be read from tables by Frank and Lee (1966).

Adjusted Monthly Temperature

Adjusted monthly temperature integrates air temperature with potential direct beam insolation.

The effect of aspect on the elevational zonation of vegetation is the basis for integrating air temperature and insolation in this study. The initial working assumption, only partly true, is that elevational displacement on a south slope is the elevational rise necessary for decreasing air temperature to compensate for the increased evapotranspirational stress resulting from more intense insolation. Actually, increase in precipitation with elevation reduces that displacement.

Whittaker and Niering (1965) indicated that on Mount Graham in Arizona the lower "boundary" of spruce-fir forest averages about 900 feet higher on south slopes than on similar north slopes. Assuming a temperature lapse rate for the warm half of the year similar to that of western Colorado (table 2)— 4.5° F. per 1,000 feet—the temperature difference is 4° F. for the 900-foot difference in elevation.

Assume an average gradient of 40 percent (Mount Graham is steep). For the period from mid-April to the end of October—from about the breakup of the snowpack to the beginning of cold weather—the difference in the potential direct beam insolation between north and south slopes would average 205 ly per day. If 900 feet of elevation difference or 4° F. is necessary to compensate for 205 ly, then a difference of 1 ly per day is equivalent to about 0.02° F. of air temperature in its apparent effect on transpiration stress.

Aridity timberline was studied on a large-scale topographic map with a green forest overprint for a foothills area in northern Colorado. Timberlines were examined on the map for regularity and for response to draws and to changes in aspect, in an effort to determine where timberline was primarily a response to climate.

Using the lapse rate for the warm half of the year (table 2, eastern subregion), a difference of 1 ly per day seems equivalent to 0.015° F. In the foothills, however, north-slope forests at their lower limits usually are well stocked, often with considerable Douglas-fir, while south-slope forests usually are open stands of ponderosa pine near their lower limits. If the lower limits of well-stocked forests were compared, a difference of 1 ly per day probably would be equivalent to about 0.02° or 0.025° F.

But precipitation also increases with elevation. If it did not, the timberline contrast between north and south slopes would be greater. Therefore, for integrating air temperature with potential direct beam insolation, it is assumed that a difference of 1 ly per day is equivalent to 0.03° F.

For any month the potential direct beam insolation on a horizontal surface at 38° north latitude was taken as a regional reference assumed to represent conditions for which Thornthwaite and Mather's (1967) water balance tables are valid. Any difference between that regional reference and the monthly insolation value of a specific habitat was used here to adjust the monthly temperature of the habitat. For example, consider a site whose normal July air temperature is 60° F. and whose daily potential

direct beam insolation for July averages 1,089 ly. That is 100 ly higher than the regional reference value for July. Because $100 \text{ ly} \times 0.03^\circ \text{ F. per ly} = 3^\circ \text{ F.}$, the adjusted July temperature is 63° F.

Climate-Soil Moisture Index

The climate-soil moisture index was adapted from Thornthwaite and Mather's (1957) soil moisture deficit, and makes use of their tables. Their moisture deficit was expressed in inches of water. Because it has been necessary here to deviate somewhat from their procedures, however (steps 1, 3, and 4 below), the resulting value does not define a quantity of water. For this reason and because soil moisture in the mountains is also influenced by net runoff, the term soil moisture deficit has been replaced here by an abstract climate-soil moisture index.

The climate-soil moisture index was determined through the 10 steps described below, with an example shown in table 3. The tables referred to in the following instructions are in Thornthwaite and Mather (1957), unless otherwise indicated.

1. Monthly HEAT INDEXES were read from their table 1, using the adjusted monthly temperature.
2. The monthly heat indexes were summed to get the annual heat index.
3. UNADJUSTED DAILY POTENTIAL EVAPOTRANSPIRATION was read for each month from their table 3, entering the table according to annual heat index and adjusted monthly temperature. Their table 3 can be used only for heat indexes of 25 or higher. When the annual heat index was less than 25, extrapolated values were used (my table 4).
4. ADJUSTED POTENTIAL EVAPOTRANSPIRATION (PE) was calculated for each month. Thornthwaite and Mather (1957) do this by multiplying the unadjusted daily values by the possible monthly duration of sunlight in 12-hour units for each degree of latitude. This adjusts for length of day and of month. Because day length had already been allowed for when adjusting monthly temperature for potential direct-beam insolation, however, adjusted PE for the month was calculated in this study by multiplying unadjusted daily potential

Table 3.--Calculation of the climate-soil moisture index for plot 32
(water-holding capacity, 12 inches)

Item	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Adjusted temperature, °F	19.2	22.7	27.0	37.8	46.3	54.4	60.5	59.0	54.3	44.1	30.3	23.0
Heat index	0	0	0	.51	2.02	3.97	5.73	5.28	3.95	1.56	0	0
Unadjusted potential evapotranspiration	0	0	0	.03	.06	.09	.11	.11	.09	.06	0	0
Adjusted potential evapotranspiration (PE)	0	0	0	.90	1.86	2.70	3.41	3.41	2.70	1.86	0	0
Precipitation (P)	2.53	2.92	3.20	1.91	1.30	1.21	2.05	2.81	2.01	2.16	2.00	2.21
P-PE	2.53	2.92	3.20	1.01	-.56	-1.49	-1.36	-.60	-.69	.30	2.00	2.21
Accumulated potential water loss					.56	2.05	3.41	4.01	4.70			
Soil moisture storage	12.00	12.00	12.00	12.00	11.45	10.11	9.03	8.58	8.10	8.40	10.40	12.00
Change in soil moisture					-.55	-1.34	-1.08	-.45	-.48			
Actual evapotranspiration (AE)	0	0	0	.90	1.85	2.55	3.13	3.26	2.49	1.86	0	0
Climate-soil moisture index (AE-PE)					-.01	-.15	-.28	-.15	-.21			

Table 4.--Unadjusted daily potential evapotranspiration extrapolated from Thornthwaite and Mather (1957)

Mean month- ly temp. °F	Annual heat index						Mean month- ly temp. °F	Annual heat index					
	10.0	12.5	15.0	17.5	20.0	22.5		10.0	12.5	15.0	17.5	20.0	22.5
32.0	0.00	0.00	0.00	0.00	0.00	0.00	49.0	0.09	0.08	0.08	0.08	0.07	0.07
32.5	.01	.01	.01	.00	.00	.00	49.5	.09	.09	.08	.08	.07	.07
33.0	.01	.01	.01	.01	.01	.00	50.0	.09	.09	.08	.08	.08	.07
33.5	.02	.02	.01	.01	.01	.01	50.5	.09	.09	.08	.08	.08	.08
34.0	.02	.02	.02	.02	.01	.01	51.0	.09	.09	.09	.09	.08	.08
34.5	.02	.02	.02	.02	.02	.02	51.5	.09	.09	.09	.09	.09	.08
35.0	.02	.02	.02	.02	.02	.02	52.0	.09	.09	.09	.09	.09	.08
35.5	.03	.02	.02	.02	.02	.02	52.5	.09	.09	.09	.09	.09	.09
36.0	.03	.03	.02	.02	.02	.02	53.0	.10	.09	.09	.09	.09	.09
36.5	.03	.03	.03	.03	.02	.02	53.5	.10	.10	.09	.09	.09	.09
37.0	.04	.03	.03	.03	.03	.02	54.0	.10	.10	.10	.09	.09	.09
37.5	.04	.04	.03	.03	.03	.03	54.5	.10	.10	.10	.09	.09	.09
38.0	.04	.04	.04	.03	.03	.03	55.0	.11	.10	.10	.10	.09	.09
38.5	.05	.04	.04	.04	.03	.03	55.5	.11	.11	.10	.10	.10	.09
39.0	.05	.05	.04	.04	.04	.03	56.0	.11	.11	.11	.10	.10	.10
39.5	.05	.05	.04	.04	.04	.04	56.5	.11	.11	.11	.10	.10	.10
40.0	.06	.05	.05	.04	.04	.04	57.0	.11	.11	.11	.11	.10	.10
40.5	.06	.06	.05	.05	.04	.04	57.5	.11	.11	.11	.11	.11	.10
41.0	.06	.06	.05	.05	.05	.04	58.0	.12	.11	.11	.11	.11	.11
41.5	.06	.06	.06	.05	.05	.04	58.5	.12	.12	.11	.11	.11	.11
42.0	.06	.06	.06	.06	.05	.05	59.0	.12	.12	.12	.11	.11	.11
42.5	.06	.06	.06	.06	.05	.05	59.5	.12	.12	.12	.12	.11	.11
43.0	.06	.06	.06	.06	.06	.05	60.0	.12	.12	.12	.12	.11	.11
43.5	.06	.06	.06	.06	.06	.06	60.5		.12	.12	.12	.12	.11
44.0	.07	.06	.06	.06	.06	.06	61.0		.12	.12	.12	.12	.12
44.5	.07	.06	.06	.06	.06	.06	61.5			.12	.12	.12	.12
45.0	.07	.07	.06	.06	.06	.06	62.0			.12	.12	.12	.12
45.5	.07	.07	.07	.06	.06	.06	62.5			.13	.12	.12	.12
46.0	.07	.07	.07	.07	.06	.06	63.0				.13	.12	.12
46.5	.07	.07	.07	.07	.07	.06	63.5					.13	.12
47.0	.08	.07	.07	.07	.07	.06	64.0						.13
47.5	.08	.07	.07	.07	.07	.07							
48.0	.08	.08	.07	.07	.07	.07							
48.5	.08	.08	.08	.07	.07	.07							

evapotranspiration from step 3 by the number of days in the month.

5. For each month, PRECIPITATION MINUS PE (P-PE) was calculated and the negative values indicated.
6. ACCUMULATED POTENTIAL WATER LOSS was calculated by accumulating the negative monthly values of P-PE.
7. Monthly MOISTURE STORAGE was read from their appropriate table (tables 11-22). The table to use is determined by the WHC of the soil. Monthly moisture storage estimates the moisture retained in the soil, or in snow potentially available to the soil, after the potential water loss accumulated through that month has been allowed for. It accounts for WHC and for the

decreasing rate at which a drying soil gives up water.

8. CHANGE IN SOIL MOISTURE was calculated for each month in which P-PE is negative, by subtracting the moisture storage of each month from the moisture storage of the previous month.
9. ACTUAL EVAPOTRANSPIRATION (AE) was calculated. For months in which P-PE is positive or zero, $AE = PE$. For the other months, AE equals precipitation plus change in soil moisture, and is smaller than PE.
10. CLIMATE-SOIL MOISTURE INDEX equals the sum of monthly $AE - PE$ for all months prior to October, and is negative. For most plots, $AE - PE = 0$ from October

until spring. For some plots, however, AE in October still is less than PE; on a few plots it is appreciably less. Most aspen leaves in the region have fallen or at least turned by early October, however, so it is assumed that an October soil moisture deficit is of little direct significance to aspen.

Runoff

Efforts described in the literature to account for the effect of runoff on height growth have included defining topographic position in terms of ridge top, upper slope, etc., in conjunction with steepness (Weitzman and Trimble 1955, Trimble and Weitzman 1956, Loucks 1962, Takeshita et al. 1966). Myers and Van Deusen (1960) found that site index in the Black Hills decreased with increasing steepness in areas of crystalline rocks, though not in limestone areas. On the other hand, in fine-textured soils in the hill country of southern Ohio, Carmean (1965) found higher site indexes on steeper slopes. He ascribed this to improved drainage and aeration.

In the Black Hills, Myers and Van Deusen (1960) also found a significant relationship between ponderosa pine site index and the distance of the plot down the slope as a percentage of total slope length. In the present study, however, slopes of substantial length commonly were complex. Much of the total slope length above a plot often does not drain through the plot because of topographic irregularities.

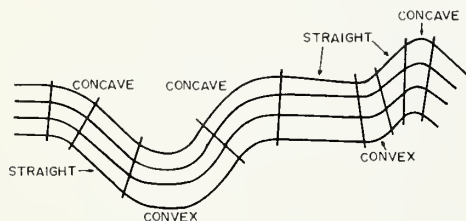
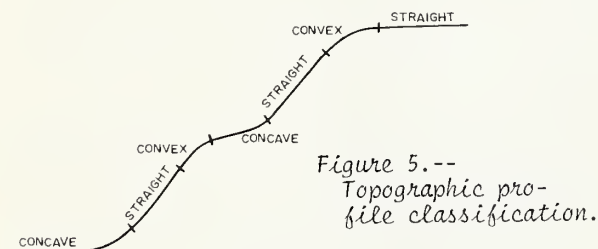


Figure 6.--Topographic contour classification.

Moisture from some distance upslope tends to become concentrated and sidetracked in surface and subsurface streams. Also, data graphed by Hewlett (1961a) suggest that the effect of increased downslope distance on capillary soil moisture content begins to decrease after as little as 20 feet.

Ideally it is desirable to express runoff at a site as a positive or negative element of the monthly moisture income. It is a complex function of many variables. Water moves through the mantle tributary to the site at different rates. Water in the system of connected large pores moves downslope fairly rapidly. Water held in the mantle by forces greater than about 1/3 atmosphere also moves downslope in quantities quite important to growing conditions, but much more slowly (Hewlett 1961a, 1961b; Hewlett and Hibbert 1963). Various factors influence net monthly runoff at a site, among them the size and vertical distribution of the area tributary to the site; the hydrological characteristics of the mantle on the tributary area, including its WHC, its porosity and its gradients; the permeability of the consolidated substrate; the normal size and time of moisture surpluses and deficits on the tributary area and on the site; and the WHC of the site.

The complexity of the processes and the lack of data and techniques for dealing with them prohibited treating net runoff as part of the monthly moisture income of a site. Instead, runoff was expressed in this study as a simple abstract runoff index incorporating a topographic index and an index of moisture surplus. The topographic index is an effort to express the ability of the terrain to permit runoff to or from a site. The moisture surplus index is an effort to express the ability of the climate to provide water for runoff.

Topographic Index

It was assumed that, with a given moisture surplus available, the amount of capillary runoff water in the soil was the result of the difference of inflow from outflow, and was largely controlled by slope shape. A corollary assumption was that gravity water is too transient in the soil to be important to aspen growth except where it results in an accessible water table.

Topography may be convex, straight, or concave in profile (fig. 5) and also in contour (fig. 6). As defined by Choate (1961), convexity tends to disperse water, concavity to concentrate it, and straightness tends to be

neutral. Flats on tablelands he classes as convex. Generally, however, tableland habitats have sufficient topographic irregularity to be classed on the basis of the immediate terrain irrespective of their tableland location. Choate classed level areas in bottoms and on benches as concave in profile rather than straight, and the same policy was followed here.

Whether curvature and scale were sufficient to class a slope as convex or concave rather than straight was decided subjectively.

Convexity was given a value of 0, straightness 1, and concavity 2. The sum of the profile value and the contour value equals the topographic index of a site. The highest possible topographic index was 4 and the lowest 0.

Moisture Surplus Index

In developing the climate-soil moisture index earlier, monthly values of moisture storage were calculated. When moisture storage equals WHC, any subsequent positive values of P-PE might be considered surplus and eventually available for runoff. Over the area tributary to the site, however, water-holding capacities may differ considerably from those on the site. Therefore, when calculating moisture surplus index, a standard WHC of 5 inches was used. The moisture surplus index is the largest monthly moisture surplus (occurring about at winter's end), computed from the accumulated potential water loss for the site but a WHC of 5 inches, as shown in table 5.

The moisture surplus index assumes a correlation between the climate of the site and that of the tributary area. It is an abstract index and not inches of water.

Runoff Index

It was assumed that the influence of runoff on soil moisture is less than linear. Some runoff reaches streams or ground water too quickly to be significant to plants; the proportion was assumed to increase with increasing moisture surplus. In combining topographic index and moisture surplus index, therefore, the runoff index was assumed to increase as the square root of the moisture surplus index.

Each successive increase in topographic index was assumed to double the runoff index.

Table 6 gives the runoff index for topographic values of 1-4; a topographic value of 0 was assigned a runoff index value of 0 regardless of the moisture surplus.

Plots with soil depth defined by a water table were given a runoff index of 8, regardless of topographic situation. That is equal to the highest value on any plot without accessible ground water, and is equivalent to a very favorable topographic situation (topographic index 3) combined with abundant water available for runoff (moisture surplus index 16). Higher values could have been chosen. The reasoning behind the selection of 8 was as follows:

1. Aspen occurs along streams below the forest zone.

Table 5.--Calculation of the moisture surplus index for plot 32, using the standard 5-inch water-holding capacity

Item	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
P-PE ¹	2.53	2.92	3.20	1.01	-0.56	-1.49	-1.36	-0.60	-0.69	0.30	2.00	2.21
Accumulated potential water loss ¹					.56	2.05	3.41	4.01	4.70			
Soil and snow moisture storage ²	8.96	11.85	15.08	16.09	4.46	3.29	2.49	2.20	1.92	2.22	4.22	6.43
Moisture surplus index ³				11.09								

¹Taken from table 3.

²From table 16 in Thornthwaite and Mather (1957).

³Maximum storage value (16.09) minus standard 5-inch water-holding capacity.

Table 6.--Runoff index

Moisture surplus index	Topographic index				Moisture surplus index	Topographic index				Moisture surplus index	Topographic index			
	1	2	3	4		1	2	3	4		1	2	3	4
0	0	0	0	0	9.0	1.5	3.0	6.0	12.0	18.0	2.1	4.2	8.5	17.0
.5	.4	.7	1.4	2.8	9.5	1.5	3.1	6.2	12.3	18.5	2.2	4.3	8.6	17.2
1.0	.5	1.0	2.0	4.0	10.0	1.6	3.2	6.3	12.6	19.0	2.2	4.4	8.7	17.4
1.5	.6	1.2	2.4	4.9	10.5	1.6	3.2	6.5	13.0	19.5	2.2	4.4	8.8	17.7
2.0	.7	1.4	2.8	5.7	11.0	1.7	3.3	6.6	13.3	20.0	2.2	4.5	8.9	17.9
2.5	.8	1.6	3.2	6.3	11.5	1.7	3.4	6.8	13.6	20.5	2.3	4.5	9.1	18.1
3.0	.9	1.7	3.5	6.9	12.0	1.7	3.5	6.9	13.9	21.0	2.3	4.6	9.2	18.3
3.5	.9	1.9	3.7	7.5	12.5	1.8	3.5	7.1	14.1	21.5	2.3	4.6	9.3	18.5
4.0	1.0	2.0	4.0	8.0	13.0	1.8	3.6	7.2	14.4	22.0	2.3	4.7	9.4	18.7
4.5	1.1	2.1	4.2	8.5	13.5	1.8	3.7	7.3	14.7	22.5	2.4	4.7	9.5	19.0
5.0	1.1	2.2	4.5	8.9	14.0	1.9	3.7	7.5	15.0	23.0	2.4	4.8	9.6	19.2
5.5	1.2	2.3	4.7	9.4	14.5	1.9	3.8	7.6	15.2	23.5	2.4	4.8	9.7	19.4
6.0	1.2	2.4	4.9	9.8	15.0	1.9	3.9	7.7	15.4	24.0	2.4	4.9	9.8	19.6
6.5	1.3	2.5	5.1	10.2	15.5	2.0	3.9	7.9	15.7	24.5	2.5	4.9	9.9	19.8
7.0	1.3	2.6	5.3	10.6	16.0	2.0	4.0	8.0	16.0	25.0	2.5	5.0	10.0	20.0
7.5	1.4	2.7	5.5	11.0	16.5	2.0	4.1	8.1	16.2					
8.0	1.4	2.8	5.7	11.3	17.0	2.1	4.1	8.2	16.5					
8.5	1.5	2.9	5.8	11.7	17.5	2.1	4.2	8.4	16.7					

2. Aspen along streams presumably draws upon ground water.
3. Aspen below the forest zone is subject to relatively high transpiration stress.
4. Such aspen is small.
5. Its restricted height growth is probably due largely to moisture stress.
6. The moisture regime ordinates for such habitats should approximate those of plots with poor height growth in the lower part of the aspen zone and without accessible ground water—about 3 to 6.
7. Water table plots should be given a runoff index which, when combined with the climate-soil moisture indexes of low-elevation aspen outliers, gives a moisture regime ordinate of 3 to 6.

The climate of Gunnison, Colorado, was used to represent one of the driest climates in which aspen is found along streams in the region. Although often very cold in winter, Gunnison has relatively warm summer days and is dry at all seasons. The characteristic upland vegetation is sagebrush and grass. Its climate-soil moisture index is -8.07. The WHC used for calculation was 4 inches, representative of soils whose depth is restricted by ground water.

A runoff index of 8, combined with a climate-soil moisture index of -8.07, gives a moisture regime ordinate of 5.2, as explained in the next section. That fits the limits decided on in item 7 above.

Moisture Regime Ordinate Chart

The moisture regime ordinate of a plot can be read from a chart (fig. 7) at the intersection of the climate-soil moisture index and the runoff index. The rationale of the chart is this:

1. If the climate is so moist that actual evapotranspiration always equals potential evapotranspiration, the moisture regime ordinate should be at the maximum regardless of the runoff index. Therefore that maximum moisture regime ordinate would be a vertical line at the right of the chart.

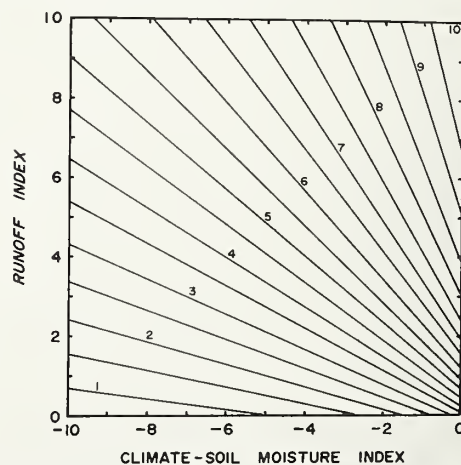


Figure 7.--Diagram for determining the moisture regime ordinate.

2. Runoff index remains a factor in aspen growth in all areas studied, however.
3. Runoff index is most important where the climate-soil moisture index is driest. The importance of runoff index can be increased on the chart by letting the lines defining the moisture regime ordinate approach horizontal.
4. If a defining line was fully horizontal, however, no importance at all would be given the climate-soil moisture index. A plot with a shallow soil and a dry climate would be assigned the same moisture regime ordinate as a plot with a deep soil and a wet climate if both had a topographic index (and consequently a runoff index) of 0.
5. Because of considerations 1 through 4, the lines defining the moisture regime ordinate were permitted to approach but not attain both the vertical and the horizontal, by radiating them from a hypothetical off-chart coordinate (1.95, -1). Thus the lowest moisture regime value, 1, falls along a line approaching horizontal (8°). The line of highest value, 10, touching the chart at the upper right hand corner, approaches vertical (80°). A convenient 8° of arc separate integral defining lines. This permits runoff index some influence on the moisture regime ordinates of relatively moist climates and deep soils. That influence increases at an increasing rate with decreasing climate-soil moisture indexes.

ASPEN SITE INDEXES

Fifty-seven plots sampled a wide diversity of aspen habitats in the region. There were two more plots outside the region in the White Mountains of Arizona. In this study, plots do not refer to areas of ground; each was simply a location with the necessary sample trees standing very near one another.

A height growth curve was drawn for each plot, from stem analysis of three dominant aspens. Site index was the height 80 years after reaching breast height, as read from the curve. A few plots were in stands younger than 80 years. Their site indexes were determined from breast-height age by means of a standard site index table (Jones 1966).

The linear multiple regression of aspen site index (S) on the temperature regime ordinate (T) and the moisture regime ordinate (M) is:

$$S = 2.41 + 0.2185 T + 4.333 M.$$

The partial regression of site index on the temperature regime ordinate was statistically

significant at about the 2 percent level. The partial regression on the moisture regime ordinate was significant at below the 0.1 percent level. Combined, the two ordinates accounted for 30 percent of the site index variance, and the equation predicted site index with a standard error of 11.5 feet. Those statistics do not actually evaluate the model, however, because the interplot habitat differences are very largely confounded by interclonal genetic differences.

DISCUSSION OF THE MODEL

Plots with the same temperature-moisture coordinate are implied to be effectively similar habitats so far as aspen height growth is concerned. If true, genetically identical aspen growing on them would give closely similar site indexes. According to the weaknesses of the numerous assumptions and approximations incorporated in the model, they would fall more or less short of that ideal.

In constructing the model, various assumptions were made. Some were selected over feasible alternatives; others were accepted only because no real alternatives were recognized. A few of them will be discussed in the remaining sections. The central assumptions in empirical soil-site equations were largely avoided.

Some plots had measured site indexes that were much different than the model indicated. Data from those plots were examined for evidence of specific weaknesses in the model, but clonal differences made the examination unproductive.

Temperature Regime Ordinate

The temperature regime ordinate is much the simpler of the two. The assumptions incorporated in it include three that seem important and uncertain:

1. Aspen trees begin the physiological processes resulting in growth when the annual course of daily maximum temperatures passes a certain "threshold" temperature.
2. Within the range of temperature climates sampled, the complex of physiological events eventually expressed as height growth intensifies linearly with the amount by which the daily maximum temperature exceeds the threshold temperature.

This assumption cannot be evaluated, but at best it would only be approximately

true, even for the cool summers of aspen forests in the region. Many individual physiological processes approximate cubic functions of temperature.

3. The important temperature responses that are expressed as height growth stop at the same temperature as they (presumably) start, unless some other factor becomes limiting.

Moisture Regime Ordinate

Construction of the moisture regime ordinate was much more complex than construction of the temperature regime ordinate, and involved more assumptions and approximations.

The moisture regime ordinate integrates runoff index and the climate-soil moisture index (fig. 7). Different combinations of those indexes can provide the same ordinate, reflecting the assumption that different combinations of climate, soil, and topography can provide the same effective moisture conditions.

Consider two hypothetical plots within the range of conditions sampled in this study, one plot with a runoff index of 3.2 and a climate-soil moisture index of 0.4; and the other with 8.0 and 3.1. With these very different indexes, both plots are assigned the moisture regime ordinate 7.6. There is no evidence demonstrating that the two plots actually have closely similar moisture conditions. It is only a working assumption based on general information about the factors involved.

Furthermore, the climate-soil moisture index of the first hypothetical plot, 0.4, could result from various combinations including a wet summer climate on a deep nearly level soil, or a merely moist summer climate on a steep north slope with shallow soil. There are no data showing that these combinations result in closely similar moisture conditions. Their common index results from several working assumptions integrating general information about climate and soil.

The climate-soil moisture index reflects factors controlling soil-moisture deficits. In part of the region that deficit develops early, during a spring and early summer that normally are very dry but are followed by rather wet weather. In the northeastern part of the region, however, spring normally is the wettest season, and moisture deficits usually peak in late summer. The time when maximum deficits develop is also influenced by slope and aspect. The same maximum deficit occurring in different

parts of the vegetative season may have appreciably different effects on height growth.

The standard errors of the estimates of average monthly precipitation and average monthly temperature indicate two other sources of error in the ordinate.

Water-holding capacity of the soil is an important variable in the moisture regime ordinates of plots with topographic indexes of two or less and without accessible ground water, especially for those with relatively warm summers or with high summer values of direct beam insolation. Using published averages of available water capacity for soil textural classes introduced significant inaccuracies, as indicated by their standard deviations (Broadfoot and Burke 1958). Leaving out organic matter content and bulk density added to those inaccuracies.

As far as the tree is concerned, any definition of soil depth is rough and arbitrary except where some physical limit to root depth can be recognized, such as bedrock or water table. Even bedrock contains roots in fractures, and water table fluctuates.

The topographic index greatly simplified the obscure complexity of runoff hydrology; it also was treated as a discontinuous variable (table 6), although it is not. A few plots were marginal, and it was difficult to assign topographic indexes to them. Their moisture regime ordinates could differ substantially depending on which index was assigned.

Steepness was disregarded in accounting for runoff, but this does not seem to have hurt the model. Although the site index equation gave gross overestimates on 3 steep plots, 7 of the 15 steepest plots are underestimated. The steepest of all plots is on a straight slope of 70 percent, but is overestimated only moderately. Nearby is a companion plot with a straight slope of 31 percent but with a very similar soil, aspect, and elevation. They appeared to be occupied by the same clone. Their actual site indexes differ by only 4 feet.

Site indexes of all four water table plots were overestimated.

Finally, internal drainage of the soil on nearly level plots was not incorporated in the moisture regime ordinate. Because most of the plots had either significant slopes or permeable substrates it was felt that this omission was not serious, but it may have contributed to site index anomalies on a few plots.

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APPENDIX

Temperature Subregions

The eastern subregion includes the more easterly parts of the mountains of Colorado and southern Wyoming. The larger western subregion comprises the mountains and tablelands farther west in Colorado. The highlands of northern New Mexico make up the southern subregion. These subregions differ in only one way from Baker's (1944) mountain climate regions 24, 23, and 25, respectively. The northern boundary of his region 25 is north of the Colorado-New Mexico border. He did not define it firmly because in nature it is a gradient and not a real discontinuity. In this study, however, the State line was used as the boundary to facilitate assigning weather stations and plots to subregions.

The boundary between the eastern and western subregions follows the Continental Divide southward from the northern end of the region to Marshall Pass; then eastward across Poncha Pass to the crest of the Sangre de Cristo Mountains; then southward along the crest of the Sangre de Cristos to the New Mexico line.

Independent Variables in the Final Precipitation Equations

Elevation.—The station elevation to the nearest 100 feet. The elevation of Santa Maria Reservoir, 9,706 feet, was recorded 97.

Latitude.—The station latitude to the nearest 0.1°. The latitude of Red Feather Lakes, 40° 47' N, was recorded 40.8.

Relief.—From each station 12 equally spaced 3-mile radii were examined on a map overlay. On each radius the highest elevation was recorded. The four highest elevations were aver-

aged. The station elevation was subtracted from the average elevation. The remainder, expressed in hundreds of feet, was the relief value.

Barriers.—Two circles were described around each station, with radii of 10 and 100 miles. The circles were divided into six sectors of 60°, based on east-west diameter and designated the N, ENE, ESE, S, WSW, and WNW sectors. Through each sector were four equally spaced sample lines which were radii of the large circle. On each sample line the highest elevation between the two circles was recorded. The two lowest of those four elevations were averaged. The station elevation was subtracted from that average elevation. The remainder, expressed in hundreds of feet was the barrier value for the sector. Barrier values of 0 or less were called 1 (that is, 100 feet) to avoid 0 or negative interaction values.

The Precipitation Subregions

The temperature subregions were not used in the precipitation analysis. There were too few high-elevation stations in northern New Mexico with long enough records to treat that area separately. Instead, an eastern and a western subregion were defined, separated as follows:

The Continental Divide from the northern end of the region south to Marshall Pass; then eastward across Poncha Pass to the crest of the Sangre de Cristo Mountains; then southward along the crest of the Sangre de Cristo Mountains to the New Mexico line; then west along the New Mexico line to the divide between the Conejos and Los Pinos Rivers; then along that divide westward to the Continental Divide; then southward along the Continental Divide to the southwestern boundary of the region.

Jones, John R.

1971. An experiment in modeling Rocky Mountain forest ecosystems. USDA Forest Serv. Res. Pap. RM-75, 19 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado 80521.

This prototype model consists of a temperature regime ordinate, a moisture regime ordinate, and a regression equation relating them to aspen site index in the Southern Rocky Mountains. Its construction required a close look at a number of problems and considerations, and some possible methods, in ecosystem modeling. Clonal variation in aspen height growth prevented a good test of the model, however.

The temperature regime ordinate is analogous to degree-days, and integrates elevation and latitude within subregions. The moisture regime ordinate integrates estimates of monthly precipitation, monthly mean temperatures, potential direct-beam insolation, water-holding capacity of the soil, and factors influencing runoff. Equations are provided for estimating mean monthly precipitation, based on topographic and other factors.

Key Words: Ecosystems, modeling, Southern Rocky Mountains, moisture regime, temperature regime, site index, precipitation estimates

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